

ON THE ORIGIN OF CARAGANA SINICA¹

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THE SHRUB LONG KNOWN as *Caragana chamlagu* Lam. probably was introduced to Europe by Father Pierre d'Incarville, who sent seed of many plants collected near Peking, China, to the Jardin des Plantes, Paris, in the period 1740–1756 (Bretschneider, 1898). Loudon (1844) stated that the species was introduced to Great Britain in 1773. Apparently it has remained since the eighteenth century one of the less commonly cultivated shrubs. Rehder (1941) has pointed out that the overlooked epithet *Robinia sinica* of Buc'hoz has priority over that of Lamarck and, to avoid confusion, the name *Caragana sinica* (Buc'hoz) Rehder will be used exclusively hereafter, although Komarov, Pojarkova, *et al.* have treated this entity under the name *C. chamlagu*. Chiefly on the basis of flower and calyx size, Pojarkova (1945) has divided *C. sinica*, *sensu lato*, into *C. sinica* and *C. ussuriensis*.

Caragana sinica, *sensu lato*, occurs widely in eastern China and far-eastern Siberia. It is a shrub 1–2 m. tall, apparently common in dry, rocky, or other well-drained sites. The leaves consist of 2 pairs of leaflets, usually pinnately arranged, but often so close together as to appear almost palmate; the leaflets are obovate, 10–35 mm. long, 5–15 mm. broad, rather coriaceous, glaucous above, the base cuneate, the apex retuse, mucronulate. The leaf rachis thickens and develops into a spine up to 25 mm. long which persists after the leaflets drop. The persistent rachises and the spiny stipules (5 mm.) give the bush its conspicuous spiny character. The flowers are large, 20–30 mm. long; the calyx 9–14 mm. long, 5–6 mm. broad, with lobes 2–3 mm. long; the pedicel attachment asymmetrical; and the calyx almost gibbous. The flowers are borne one or two per node on stalks 10–20 mm. long, articulated in the middle between pedicel and peduncle. The corolla is pale yellow, usually with a rose or bronze tinge which deepens with age.

It is generally agreed that *Caragana frutex* and related species comprise the only species-group to which *C. sinica* is clearly related. Komarov (1908) placed *C. sinica* in his series FRUTESCENTES. He recognized its unique character and regarded it (*loc. cit.*, p. 370) as the closest claimant to the position of generic prototype. He based this view on its leaf character, noting that at an early age the leaf is palmate but later becomes pinnate. This transition he held to be a phylogenetic recapitulation, apparently regarding palmate leaves as ancestral to pinnate. Although not clearly stated, it appears that Komarov did not refer to the form of early seedling leaves but to the varying forms seen on adult plants. He believed

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(p. 371) that different environmental conditions then had resulted in the evolution from *C. sinica* of both palmate-leaved species (FRUTESCENTES) and pinnate-leaved species (ALTAGANAE) and subsequently from these, all the other series. *Caragana sinica* thus assumes special importance as the foundation of Komarov's phylogenetic scheme. Doubtless as a result of this opinion, he designated east Asia (range of *C. rosea*, *C. fruticosa*) as the primary center of species formation.

To show specific relationships more exactly, Pojarkova (1945) divided the series FRUTESCENTES Kom. into three more homogeneous but related series: CHAMLAGU, FRUTESCENTES *emend.*, and GRANDIFLORAE. The series CHAMLAGU Pojark. consists of *C. sinica* and *C. ussuriensis* (Regel) Pojark. The latter taxon had been described by Regel as *C. frutex* var. *ussuriensis*, and, as such, was placed in the synonymy of *C. sinica* by Komarov (1908).

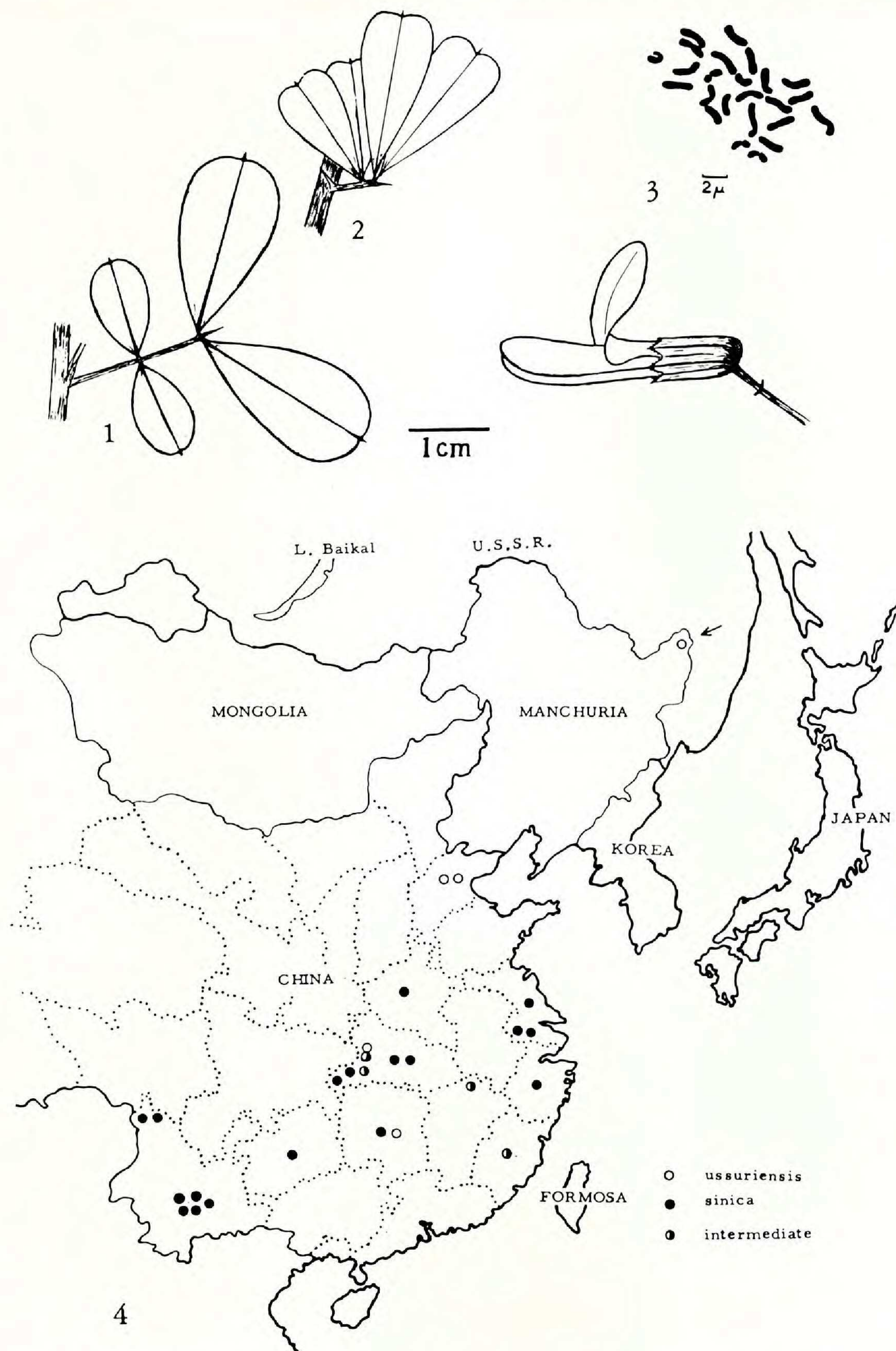
Pojarkova separates *Caragana ussuriensis* and *C. sinica* chiefly on floral characters: flower length, 23–25 mm. *vs.* 28–30 mm.; and calyx size, to 9 mm. long \times 5 mm. broad *vs.* 12–14 mm. long \times 6 mm. broad. The leaflets of *C. sinica* are said to have a broader, obovate blade and broader base, giving a more rounded outline, whereas those of *C. ussuriensis* are narrow with a narrowly cuneate base. Only *C. ussuriensis* occurs in the U.S.S.R. (region of the river Ussuri just north of Manchuria) from whence it extends southward into Manchuria and northern China. It is reported that *C. sinica* has a more southerly distribution in China: Hopeh (Chili) to Yunnan. The impression is conveyed by Pojarkova that the range of *C. ussuriensis* is more northerly than that of *C. sinica* and that, although they overlap in northern China, *C. sinica* alone occurs in southern China. The two taxa are illustrated in Figs. 1 and 2.

The illustration accompanying Buc'hoz's (1779) description of *Robinia sinica* is apparently drawn life-size and shows the larger-flowered plant. Mature open flowers are 30 mm. long, the calyx being 11–12 mm. long and 6 mm. broad, measurements which fall within the limits indicated by Pojarkova for *C. sinica*.

MATERIALS AND METHODS

In the course of a survey of chromosome numbers in *Caragana*, a special attempt has been made to obtain living material of *C. sinica*. Seeds have been received under this name from twelve botanic gardens (eleven European) but the resulting seedlings proved to be not the desired species but typical plants of *C. frutex*, *C. arborescens*, *C. pygmaea*, or *C. aurantiaca*. Some of these species are not closely related to *C. sinica*; all are readily distinguished from it and it is considered that the error is due solely to incorrect identification of the seed parent. In two cases, leaflets in the seed packet indicated that the source of the seed was *C. arborescens* and *C. pygmaea*, as were the resulting seedlings.

Living plants of *Caragana sinica* have been obtained from only one source: F. J. Grootendorst & Sons, Boskoop, Holland. The species has been propagated asexually in this nursery. It was received there at some



FIGS. 1-4. Morphological details and distribution of *Caragana sinica*. 1, Leaf and flower of *C. sinica*. 2, Leaf of *C. ussuriensis*. 3, Somatic chromosome complement of *C. sinica* (cultivated triploid). 4, Distribution of *C. sinica*, sensu lato,

time before 1928, but the source is unknown (H. J. Grootendorst, personal communication, 1961).

Cuttings of the rare species *Caragana rosea* were received from the Arnold Arboretum, Harvard University, where there is a single shrub grown from seed collected by William Purdom (seed lot 9a), in 1909, in Weichang, Chili (Hopeh) Province, China. This collection was determined as *C. rosea* by Rehder (1926).

Herbarium material of *Caragana sinica* from the Arnold Arboretum (A) and the Gray Herbarium (GH) of Harvard University and from the United States National Museum (US), as well as that in the Herbarium, Canada Department of Agriculture (DAO) has been examined. Particular attention has been paid to the characters which separate *C. sinica* and *C. ussuriensis* and to the condition and size of the pollen. Pollen was mounted in 45% acetic acid and stained with dilute cotton blue. Grains with a protoplast which completely filled the cell and stained blue were counted as viable. The grains are thin walled and smooth; the diameter stated is the measurement to the outer surfaces.

MORPHOLOGY, POLLEN CONDITION, AND NATURAL DISTRIBUTION

Little variation was found in the size of the flower on any single herbarium specimen, and it is believed that these size-characters are reasonably constant for any individual. A similar opinion has been formed from observation of numerous living plants of various species of *Caragana* over a number of years, and it is believed that the size-characters used by Pojarkova reflect genetic differences and are reliable for systematic purposes.

Following the floral and leaf characters designated by Pojarkova, 34 of 38 herbarium specimens were referred either to *Caragana ussuriensis* or to *C. sinica*. The determination of the remaining four, all wild Chinese collections, was less certain. Two had the flower size of *C. sinica* with a smaller calyx, and two had the smaller flower of *C. ussuriensis* with a calyx similar in size and appearance to that of *C. sinica*.

The localities of the Asiatic collections are plotted on the map of eastern Asia (FIG. 4) and are listed below. A few collections were omitted, either because of uncertainty about the location or because only a general area was indicated. Symbols were placed in the center of a province when data or knowledge were insufficient to place them more accurately.

It is concluded, in agreement with Pojarkova, that the small-flowered plant occurs from northern China to Siberia and that the large-flowered plant is dominant in southern China. The small-flowered plant seems to extend as far south as approximately 27° N, well into the range of the large-flowered entity, and a few intermediates were found in the zone of central China in which both entities occur.

Pollen of 34 herbarium specimens, 27 of these wild Asiatic collections, was examined, and in none was the pollen 100% normal. The samples

consisted of mixtures of normal grains with full, densely staining protoplasts; grains full but with a thinner, lightly staining content; grains only partially filled with a thin protoplast; grains empty and collapsed; and empty micro-grains. Difficulty was experienced in classifying some grains since the first two classes intergrade. Only grains with a full, dense protoplast were classed as normal in the following counts. The micro-grains probably were formed from lagging chromosomes excluded from the tetrad nuclei and indicate a high degree of meiotic irregularity.

The maximum percentage of normal pollen found among the herbarium specimens was 80, the minimum, 3; 12 lay in the range 0–39%, 14 had 40–50%; 8 had over 50%. The size of the normal grains ranged from 18 to 30 μ but this range was not found in any single sample. The modal range was 20–40 μ (13); in 6 samples the lower limit was 18–20 μ , and the upper limit was lowered correspondingly. The range in 10 samples was from 20 μ to 25–27 μ , and in 6 the smallest grains were 23 μ , the largest 27–30 μ .

Pollen measurements (unpublished) made on other *Caragana* species do not show a correlation between the diploid and tetraploid chromosome number and pollen size. The samples are almost invariably 100% normal. Pollen of seven diploid species falls in the range 20–27 μ ; two additional diploids measured 23–29 μ and 28–30 μ . Pollen of one tetraploid species (*C. frutex*) measured 20–27 μ , of another (*C. spinosa*) 24–34 μ . No correlation between pollen size, probable chromosome number, or morphological features is believed to exist in *C. sinica*, and the pollen size variability is attributed to gene differences between the various populations. The significant feature lies in the consistent absence of wholly good pollen and the similarity of the condition of all samples. No difference was found in the range of size or of fertility between specimens classed as *C. sinica*, *C. ussuriensis*, or intermediate. Pollen samples of the latter group fall in the range of 40 to 60% normal and thus were no more “hybrid” than those of the more typical groups. No certain correlation was found between the degree of pollen fertility and geographical location, although there may be a tendency for plants with the higher percentages (70% plus) to occur on the extremes of the range (Northern China and Yunnan).

Caragana sinica (Buc'hoz) Rehder, Jour. Arnold Arb. 22: 576. 1941.

Robinia sinica Buc'hoz, Pl. Nouv. Decouv. 24. t. 22. 1799.

Flowers 27–30 mm. long, calyx 11 mm. or more, leaflets broadly obovate.

China. CHEKIANG: without location, *Barchet* 146 (US). FUKIEN: Dionghloh Hsien, *Chung* 1239, Apr. 5, 1923 (A). HOPEH (Chili): Hsi Yu Ssu, *Liu* 2286, June 8, 1929 (A). HUNAN: Tschangscha, *Handel-Mazzetti* 638, Apr. 14, 1918 (A). HUPEH: W. Hupeh, *Wilson s.n.*, Apr. 1900 (US); W. Hupeh, *Wilson* 2203, May 1907 (GH); without location, *Henry* 5378 (GH), 3812 (US). KANSU(?): Fengwangschan, *Forbes* 113, Apr. 22, 1877 (A). KIANGSU: without location, *Tsu* 436, Apr. 26, 1920 (A); Yun Dai Shan, Nanking, *Tso* 79, Apr. 17, 1926

(A): without location, Faber *s.n.* (A). KWEICHOW: Kweiyang, *Teng* 90079, Apr. 15, 1936 (A). YUNNAN: East of Tengyueh, *Forrest* 19343, Apr. 1921 (A, US); Yunnanfu bei Puchli, *Schneider* 214, Mar. 7, 1914 (A); zwischen Ssiao und Schin lung, *Schneider* 4046, Mar. 9, 1914 (A, GH); without location, *Bonati* or *Maire* 7286 (US); Yunnanfu, *Smith* 1582, 8/3, 1922 (A).

Cultivated. JAPAN. Hondo: Musashi, *Teizo* 1648, July 2, 1904 (A); without location or collector, May 13, 1910 (US 1311798); Nagasaki, *Maximowicz s.n.*, 1863 (GH). FRANCE: Paris, *Gay, s.n.*, 1822 (GH). Bavaria, *Scherzer s.n.*, Apr. 1, 1906 (DAO). UNITED STATES: Washington, D.C., Apr. 24, 1886 (US 137850); Washington, D.C., 1915 (US 786433); Chico, Calif., Apr. 25, 1922, S.P.I. 22981 (originally collected in Soochow, Kiangsu, China) (A). CANADA: Royal Botanic Gardens, Hamilton, Ont., *Rhodes & Florian* 3587, June 11, 1952 (DAO); Dominion Arboretum and Botanic Garden, Ottawa, Ont. *Moore*, 53-249-1, May 27, 1960 and *Moore*, 60-231-45, May 29, 1961 (DAO); Experimental Station, Morden, Man., *Rhodes & Vitens* 4583, Sept. 10, 1953 (DAO).

Caragana ussuriensis (Regel) Pojark. *Flora U.S.S.R.* 11: 395. 1945.

Caragana frutescens β *ussuriensis* Regel, *Mem. Acad. Sci. St. Petersburg. ser.* 7. 4(4): 44. 1861.

Flowers 23-26 mm., calyx to 9 mm., leaflets narrowly obovate with cuneate base.

China. HOPEH (Chili): Western Hills, Peiping, *Chiao* 21361, May 7, 1929 (A); Nankow, Peiping, *Chiao* 21253, May 11, 1929 (A). HUNAN: Yi Chang District, *Tsang* 23430, Mar. 21-29, 1934 (A). MANCHURIA: Ussuri super, *Maximowicz s.n.*, 1860 (US). NORTH CHINA: without location, *Bunge s.n.* (GH).

Cultivated. JAPAN: without location, *Zuccarini s.n.*, 1842 (GH).

Specimens intermediate between *Caragana sinica* and *Caragana ussuriensis*.

China: HUPEH: W. Hupeh, *Wilson* 2203, May 1907 (US); Patung, *Wilson s.n.*, Apr. 1907 (A). KIANGSI: Kipkiang, *Bullock* 151, Apr. 20, 1892 (US). FUKIEN: Diongluh Hsien, *Chung* 1239, Apr. 5, 1923 (A).

CULTIVATED CARAGANA SINICA

The five plants purchased from the Grootendorst nursery are identical in appearance, doubtlessly having been propagated asexually from a single plant. Flowers are 30 mm. long, with the calyx 11-12 mm. long and 6 mm. broad. The leaflets are broadly obovate, to 20 mm. long, 9 mm. broad, coriaceous, and glaucous. On the basis of flower and calyx size and leaflet shape, the plants are to be classed as the larger-flowered species, *C. sinica* sensu Pojarkova. In all characters they are indistinguishable from collections of other cultivated and wild Asiatic plants.

CYTOLOGY. The chromosome number was determined from leaf squashes to be $2n = 24$ (FIG. 3). The basic number of the genus is 8: hence this number is triploid. Meiosis was studied in one plant growing outdoors at Ottawa. The configurations at Metaphase I could be fully analyzed in

only eight cells but these seem to be representative. The minimum pairing seen was 16 univalents and 4 bivalents; 8 bivalents and 8 trivalents were seen in two cells. The trivalent was the largest association found, and three trivalents was the maximum number found in a single cell. The average pairing for eight cells was $8^I + 6.7^{II} + 0.86^{III}$.

Approximately 40% of mature pollen grains are normal in appearance. Grains judged to be normal have a full, dense protoplast and measure 20–24 μ in outer diameter. Pollen was spread on a mixture of 2% agar plus 5% sucrose, and germination of at least 50% of these full grains was observed. This agar medium has been found to give good germination of pollen of many species of *Caragana*.

FLOWER BIOLOGY. At Ottawa, the shrubs flower from late May to mid-June, meiosis occurring in buds 5–6 mm. long in the period May 10–17. Over the past ten years it has been observed that varying weather conditions cause little variation in the onset of flowering in *Caragana* species, at most, two to three days.

Small aborted pistils were noted, but probably not over 10% of the flowers are defective. No other abnormality was observed. The style elongates markedly and extends approximately 2 mm. beyond the keel at anthesis. This feature favors cross-pollination and probably makes insect action necessary even for self-pollination. The plants studied were located approximately 100 feet from other *Caragana* bushes (*C. arborescens*, *C. frutex*, *C. aurantiaca*) and separated by various other trees and shrubs. It is highly probable that the 5 plants of *C. sinica* were not pollinated from other species. Most flowers dropped without ovary enlargement; some showed slight enlargement but dropped in two to three days. A smaller number, estimated at 8–10%, developed conspicuously enlarged ovaries (25–28 mm.) which turned green and for a week appeared to be forming seed. However, all turned brown and fell. Some of the shrubs have been observed for three years and no seed has been formed. Plants from the same source grown at the Experimental Farm, Morden, Manitoba also are sterile (personal communication). Pollen of *C. sinica* was used to pollinate shrubs of *C. arborescens*, *C. microphylla* and *C. frutex* but no seed resulted. Two of 38 flowers of *C. frutex* pollinated by *C. sinica* showed slight ovary enlargement before dropping.

OVULE HISTOLOGY. Ovaries of various sizes, pre- and post-flowering, were fixed for histological study of the ovules. Several different types of ovule development were observed, but in all cases all ovules within a single ovary were similar.

Ovaries which lacked ovules or contained abnormal and partially developed ovules were found. Undeveloped ovules consisted of a small nucellus partially enclosed by a tissue two or three cells thick which presumably represented the outer, or perhaps both integuments. This integument did not enclose the micropylar end of the nucellus. No sporogenous tissue was differentiated and all tissues appeared unhealthy. Such

ovules were found in mature open flowers, a stage when mature embryo sacs should have been present.

Structurally normal ovules were found in ovaries of some mature flowers. These ovules, approximately 525 μ long and 375 μ broad consisted of two integuments and nucellus, all apparently normal. Cell formations suggestive of aborted embryo sacs were observed in the nucellus. A linear formation of three compact cells, the micropylar one of which was the largest, was probably the product of meiosis. The innermost of the three was the most healthy and normally probably would be the functional megaspore. A large two-nucleate cell surrounded by disorganized tissue seemed to be an aborted early embryo sac. A four-nucleate cell (75 μ long, 15–20 μ broad) also was apparently an immature embryo sac. The most advanced structure seen was interpreted as a disintegrating mature embryo sac. This structure was 125 μ long, 20 μ broad and contained five recognizable nuclei and remnants of at least two antipodal cells. In all the above examples both sporophytic and gametophytic tissues were obviously in an unhealthy condition and incapable of continued development. Many ovules were so disorganized that the stage of embryo sac development could not be determined.

The large ovaries mentioned above (to 28 mm.) contained ovules that were enlarged by some 50% beyond the size of the most normal mature ovules. However, none of these contained embryos. Counts of the cell layers and measurements of representative cells indicated that ovule enlargement was due solely to cell enlargement in both the integuments and nucellus. By the time such ovaries drop, breakdown of the nucellus is advanced. A patch or narrow zone of empty collapsed cells in the area in which an embryo would normally be found is first seen. Dissolution of cell contents and collapse of the walls progresses through the middle of the nucellus from the micropylar to the antipodal end. It was usually observed that the two-celled peripheral layer of the nucellus at its micropylar end remained longest in apparently healthy condition. A zone of the inner integument adjoining the micropylar end of the nucellus appeared more active than the remainder of the integument endodermis. These observations together suggest that the integument cells at this point were absorbing the contents of the nucellus. In the final stage of ovule collapse only remnants of walls remained of the nucellus. No evidence of apomictic seed formation was observed and there is no reason to believe that these plants would ever set seed through either sexual or apomictic processes.

DISCUSSION

The occurrence of a major amount of aborted pollen in the living cultivated (Grootendorst) plant and in all known collections of *Caragana sinica* from the wild suggests that the species is of hybrid origin. Whether the species in nature is triploid, like the cultivated plant studied, cannot be decided with the available evidence.

Morphology of the species alone suggests a hybrid origin. That the leaf, which is pinnate with two pairs of leaflets, frequently appears to be palmate due to the lack of elongation of the rachis suggested to Komarov that the species was ancestral to both the pinnate and the regularly palmate series. An alternative explanation of this phenomenon is that *C. sinica* is a hybrid between a pinnate- and a palmate-leaved species. The variable-leaf type occurs otherwise only in the series SPINOSAE and DASYPHYLLAE, groups of central Asia morphologically very unlike *C. sinica*. It seems obvious that these do not bear on the present problem.

All authors agree that *Caragana sinica* is most closely related to *C. rosea* Turcz. The affinity appears in the number, shape and texture of the leaflets, the persistent spiny leaf rachis, the large flower (more than 2 cm.) which is pale yellow with a rosy tinge, and the large calyx which is longer than broad. The rose flower color is not known in other species of eastern China. *Caragana rosea* has a range in eastern Asia (Manchuria, Hopeh, Honan, Kansu, Chekiang [Rehder, 1926]) very like that of *C. sinica*.

If the hybrid nature of *Caragana sinica* is accepted, *C. rosea* must be proposed as one parent. A pinnate-leaved species of eastern China is required as the other parent, but the exact species cannot be named with an equal degree of assurance. The large flowers of *C. sinica*, larger even than those of *C. rosea*, point to another large-flowered species as the second parent. Such is to be found in *C. microphylla* Lam. (flowers 25 mm., calyx 9–12 mm.) a species of suitable leaf type and range as well.

It is therefore postulated that *Caragana sinica*, *sensu lato* (including *C. sinica* (Buc'hoz) Rehd. and *C. ussuriensis* (Regel) Pojark.) is a hybrid between *C. rosea* Turcz. and a pinnate-leaved species, probably *C. microphylla* Lam. In the opinion of the author it would be preferable to recognize the entities *sinica* and *ussuriensis* at infraspecific level under *C. sinica* (Buc'hoz) Rehd. It seems obvious that they have shared a common origin and are separated by characteristics of a minor order, quantitative rather than qualitative. The two populations have achieved geographic separation, and taxonomic recognition is justified.

A variation within *Caragana rosea* in flower and calyx size and leaflet shape, parallel to that used by Pojarkova to split *C. sinica* was noted in thirteen specimens (us) examined. These could be divided into large-flowered (flower 25–27 mm., calyx 9–11 mm.) and small-flowered (flower 20–24 mm., calyx 6–8 mm.) plants. The more rounded leaflet shape was not invariably associated with the greater flower size, nor was there an evident geographical correlation. The range in pollen size in *C. rosea* was 20–27 μ . The variation within a single plant was not more than 4 μ . However, no correlation between larger pollen size and flower size was found. The existence in *C. rosea* of variation of the same type as that seen in *C. sinica* is an additional indication of their close affinity.

The chromosome number of the single available accession of *Caragana rosea* was found to be $2n = 16$. This diploid number is surprising, since it might be expected that this species would be tetraploid like the closely related *C. frutex*. The latter was reported to be tetraploid ($2n = 32$) by

Tschechow (1930, as *C. frutescens*), and only this number has been found in nine accessions in the present work. *Caragana rosea* appears to be morphologically a more advanced species than *C. frutex*. The persistent thickened petiole seen in *C. rosea* is apparently developed from the deciduous petiole of *C. frutex*. Throughout the genus there is an evolutionary trend toward transformation of the deciduous petiole, first, to a persistent but essentially unthickened petiole and, finally, to a persistent and much thickened organ. The latter is the stout spine seen in many species. This trend is found in both the pinnate- and the palmate-leaved series.

The lower chromosome number of *Caragana rosea* can be reconciled with the view that the species is derived from *C. frutex* by postulating that diploid populations of *C. frutex* do or did exist. It is, indeed, not improbable that the series FRUTESCENTES arose at the diploid level from a pinnate-leaved ancestor. All pinnate-leaved species yet examined are diploid (Moore, 1958 and unpublished). The series FRUTESCENTES Kom. *em.* Pojark. contains six species which extend from the Black Sea to central Mongolia. Three other Chinese species not treated in the *Flora of the U.S.S.R.* but which should doubtless be referred to the series, extend the range of the series across northern China and Manchuria to the Pacific. *Caragana frutex* has by far the largest range of any single species (Black Sea to northwest Mongolia). Four species of relatively narrow distribution are found in Central Asia, south of Lake Balkhash. It seems possible that ancestral diploid "frutex" has spread from central Asia eastwards, developing in the most eastern part of the series range into *C. rosea*. The morphologically more primitive "frutex" stock may have become autotetraploid in central Asia, and, enjoying an advantage, accomplished the present wide distribution, particularly to the west and north from Central Asia. It seems probable that *Caragana frutex* in cultivation has come from the European part of the range, the western extreme, and thus is tetraploid. Diploid populations may still exist in Central Asia. Unfortunately the chromosome numbers of the more limited species of Central Asia are unknown. The range of *C. rosea* is second only to that of *C. frutex*, suggesting considerable age for the former species.

The triploid number of the Grootendorst plant of *Caragana sinica* suggests a hybrid origin between a diploid and a tetraploid species. Two serious difficulties at once arise. The tetraploid number is not known in either postulated parent species. A triploid hybrid, if at all like the Grootendorst plant, will be seed sterile, and it seems impossible that the extensive range of *C. sinica* was accomplished by any means other than by seed dispersal. Moreover, it is known that the species in China does set seed.

These difficulties may be relieved by suggesting that *Caragana sinica* in eastern Asia is diploid, a hybrid between diploid *C. rosea* and *C. microphylla*. A reduced, but still appreciable, seed fertility will then be possible. The triploid condition of the Grootendorst plant may have arisen in cultivation. The plants are morphologically indistinguishable from wild

collections, and it is therefore improbable that a cross with a different tetraploid species has occurred in cultivation. The triploid condition may, however, have developed from the fertilization of an unreduced egg. Indeed, the different climactic conditions of Europe acting on a somewhat unstable hybrid genome may have caused the formation of an unreduced gamete. By random chromosome segregation, the additional haploid set could add an equal number of chromosomes from each parent to the diploid hybrid complement, converting some former bivalents into trivalents. The presence of equal numbers from each parental species might maintain the gene balance to such a degree that the triploid appears identical with the diploid. The absence of a noticeable difference in pollen grain size between diploid and triploid may be disregarded since no correlation between chromosome number and pollen size has been observed in the genus, and it is believed that pollen size depends solely on the genes governing this character.

It may be pointed out in conclusion that the widespread occurrence of pollen abortion in *Caragana sinica* is explained better by the hybridity hypothesis than by the prototype hypothesis of Komarov. It seems improbable that an ancestral stock would have retained a condition of abortive pollen, presumably due to meiotic irregularities, which had been eliminated from its descendants.

SUMMARY

It has been possible to obtain *Caragana sinica* (Buc'hoz) Rehd. from only one source in cultivation. The plant is triploid ($2n = 24$), pollen is 40% normal, no seed is set. All herbarium specimens, of wild and cultivated collections, have partially aborted pollen. It is postulated that *C. sinica* is a hybrid between *C. rosea* Turcz. and probably *C. microphylla* Lam. The hybrid in nature is probably diploid; the triploid cultivated clone may have arisen in Europe by the production of an unreduced gamete. The chromosome number of *C. rosea* Turcz. is $2n = 16$.

The author wishes to express appreciation to the curators of the herbaria from which material was borrowed and particularly to members of the staff of the Arnold Arboretum and Gray Herbarium with whom the author has corresponded. Dr. J. L. Thomas, formerly of the Arnold Arboretum, was most co-operative in making observations and procuring specimens and cuttings of the *Caragana rosea* in the Arboretum. At the author's request, Mr. H. J. Grootendorst looked into the source of the *Caragana sinica* sold by their nursery. Dr. T. Koyama, University of Tokyo, has informed the author that collections of *C. sinica* from Japan are undoubtedly introductions.

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